Visual Target Discrimination in Blacktip Sharks (*Carcharhinus melanopterus*) and Grey Sharks (*C. menisorrah*)[1]

Albert L. Tester[2] and Susumu Kato[3]

Conditioned response experiments with juvenile blacktip (*Carcharhinus melanopterus*) and grey (*C. menisorrah*) sharks (Schultz et al., 1953) were conducted at the Eniwetok Marine Biological Laboratory, Marshall Islands, during 1960. Our objective was to investigate the sharks' visual capabilities with regard to orientation, form, differential brightness, and color discrimination of targets.

The conditioned response technique has been used only recently in the investigation of sensory perception in sharks. It was employed in auditory studies by Vilstrup (1951), Kritzler and Wood (1961), Olla (1962), Davies et al. (1963), and Wisby et al. (1964), in olfactory studies by Teichmann and Teichmann (1959), in electrical sensitivity studies by Dijkgraaf and Kalmijn (1963), and in visual studies by Clark (1959, 1961, and 1963). Clark's work on instrumental conditioning of lemon sharks is particularly pertinent to the present study.

Related studies on the anatomy and physiology of the visual system of elasmobranchs (Franz, 1913 and 1931; Verrier, 1929; Gilbert, 1963) and behavioral studies in the field (Hobson, 1963) have provided some information on the visual capabilities of sharks. However, with the exception of Clark's work, subjective methods utilizing training techniques have not been used to investigate vision in sharks.

MATERIALS AND METHODS

Subjects

The sharks used were immature blacktips and greys 19 to 33 inches in total length (Table 1) captured from reef flats adjacent to the laboratory.

Experimental Apparatus

The experimental tank was located within a larger rectangular concrete tank which could be subdivided into 5-ft sections (Tester, 1963). It was housed in a building which excluded most light, and some extraneous noise. A booth adjacent to the tank enabled the observer to view the sharks through a narrow slit 5 ft above the water without being seen by them.

The design of the experimental tank is shown in Figure 1,*A*. Dimensions were: width 4 ft, length 20 ft, and depth 3 ft. The ends were rounded with curved vertical sheets of galvanized iron. Boundaries of the end compartments consisted of notches on the walls and dark lines on the bottom. All sides and ends were painted dull black, but the bottom was brown.

A 6-inch square aperture was cut in the middle of each galvanized sheet, 12 inches below the water level. For some experiments a second square was cut with its upper edge 3 inches below the bottom edge of the first aperture. Targets were mounted on panels which, guided by grooves located behind the apertures, were manipulated from the observation booth by means of cord and pulleys. In successive discrimination training, a single aperture was used. Two targets were clipped together, one above the other, and changes were made by lowering or raising the appropriate target to the level of the aperture. When two apertures were used, in simultaneous discrimination training, three targets were clipped in series, so that the middle and either the top or bottom targets were visible through the apertures.

Paired electrodes were placed along the walls of both end sections *L* and *R*. Each electrode consisted of a brass rod to which were welded nine heavy copper wires spaced 6 inches apart, extending from the surface to within 3 inches

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[2] Department of Zoology, University of Hawaii, Honolulu, Hawaii.

[3] Presently with Bureau of Commercial Fisheries, La Jolla, California.

TABLE 1

CODE NUMBER, TOTAL LENGTH, AND SEX OF BLACKTIP (B) AND GREY (G) SHARKS

NO.	LENGTH (INCHES)	LENGTH (CM)	SEX
B1	20½	52	F
B2	21	53	F
B3	23	58	M
B4	21¼	54	M
B5	32½	82	M
B6	30½	77	F
B7	22½	57	F
B8	19	48	F
G1	31	79	M
G2	33	84	F

of the bottom. Shocking was accomplished by capacitor discharge. A coupling transformer isolated the system from the 115 volt AC line. Voltage was controlled by a Variac transformer. A fullwave selenium rectifier produced DC which charged a bank of capacitors. The charge was released by a toggle switch controlling a solenoid switch, the latter with heavy contact points. A double-pole, double-throw knife switch enabled the selection of electrode pairs at either end of the tank. The best field was produced at a charge of 90 volts, the maximum rating of the capacitors.

Visual cues were made of Munsell color standards[4] on high gloss paper, possessing known values of hue (color), value (brightness), and chroma (saturation), based on the human eye in air.[5]

All targets had an area of 9 sq inches, and consisted of white (N9/) squares, circles, equilateral triangles, and rectangles (1.8 × 5 inches), grey squares with values ranging from white (N9/) to black (N1/), and colored squares with the following characteristics: red (5R5/14), yellow (5Y5/6), green (5G5/8), blue (5B5/6), and purple (5P5/9.2). All colored targets were equal to medium grey (N5/) in subjective brightness for the average human eye. The targets were glued to panels of vinyl floor tile which had been painted dull black.

Continuous illumination was provided by a fluorescent light fixture, located about 6 ft above the center of the tank with its long axis parallel to that of the tank. Similar fixtures elsewhere in the shark house contributed only slightly to the illumination, which was measured with a Weston Illumination Meter (Model 756) with Viscor filter. The remote-measurement paddle was housed in a waterproof plexiglass covering. Incident light, measured 1 inch above the water surface at various points of the tank (Figure 1,*B*), ranged from 27 to 42 ft-c. At any point, the values varied only about 1 ft-c between day and night readings. Measurements taken below the surface of the water (1, 10, and 18 inches) showed vertical gradients from 37 to 30 ft-c in the center of the middle sections, and from 24 to 22 ft-c in the center of the end sections. At the level of the targets and immediately adjacent to them, the illumination was 11 ft-c. The light and water clarity were sufficient to allow a submerged diver with a face plate to distinguish all shapes and colors of targets from one end of the tank to the other.

Training and Testing Procedure

Sharks were trained to associate selected targets with electric shock. This was accomplished by the following procedure:

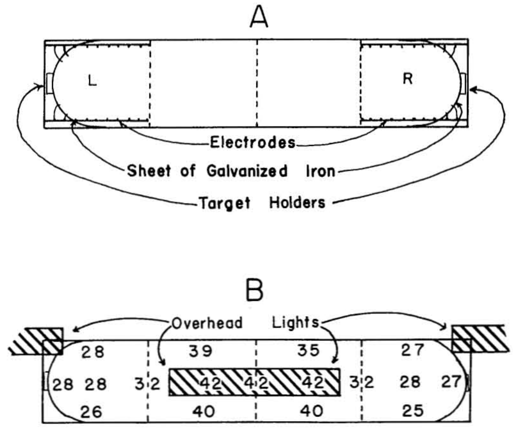

FIG. 1. *A,* Experimental tank, *B,* incident illumination one inch above the surface of the water, in foot-candles.

[4] Munsell Color Company, Inc., 2441 North Calvert Street, Baltimore 18, Maryland, U.S.A.

[5] A complete description of the system of specifying color, with graphs for conversion to other systems, is given by the American Society for Testing Materials (ASTM Standards, Part 8, 1958).

1. The neutral targets were displayed at both ends and the shark was allowed to acclimate.

2. The negative target was displayed at one end for a period of 3 min, and the shark was shocked each time it entered that end.

3. After a rest period of 3–5 min, during which the neutral targets were displayed at both ends, the procedure was repeated at the other end of the tank.

Each training session lasted from 36 to 45 min with six alternating shocking and rest periods, or 18 min of potential exposure to shock. A minimum of 2 hr was allowed between sessions. Training was continued until a shark displayed that it had made the required association, at which time a test was conducted. If after a reasonable number of training sessions the shark had not displayed signs of discrimination, training was discontinued, usually after tests had been conducted.

During test periods the negative target was displayed but no shock was administered when the shark entered the negative end.

Both simultaneous and successive discrimination training techniques (Sutherland, 1962) were employed. In the former case two neutral targets were presented, one above the other, during rest periods, one of which was replaced by a negative target during training.

Criteria of Discrimination

Abrupt changes in behavior, when occurring consistently with appropriate target changes, were considered to be end points of behavior indicating that the shark had made the desired associations, and hence discrimination between the negative and neutral targets. The following are such behavioral changes, one or several of which occurred with individual sharks: (1) head-shaking or body-quivering on facing the negative target for the first time at the start of a training period or during a test period; (2) a sudden swirl or an abrupt change of swimming pattern on presentation of the negative target; (3) turning from the negative target before being shocked, either consistently or at least during the first few passes of each training period, or during test periods; (4) following this behavior, entering the end zone immediately after the negative target had been replaced by the neutral target; (5) sudden dashes into and out of the negative end zone immediately after the target was displayed; (6) dashing toward the negative target and abruptly turning at the line marking the entrance; (7) abrupt decrease in excitability when the target was changed to neutral, or abrupt increase in excitability when the negative target was presented.

RESULTS

Using the criteria listed above, sharks were subjectively judged to have succeeded or failed to discriminate between negative and neutral targets. Results of all experiments are summarized in Table 2; the total training time (including shocking but not control periods) and number of training sessions are entered in Table 3. In cases of positive conclusion, the times and sessions represent training until discrimination was evident. In all such cases additional training confirmed the results.

Some sharks (marked ? in Table 2) displayed good signs that they could discriminate, but their over-all behavior was too erratic to afford a firm conclusion. The implication is that further training might possibly have strengthened the association.

Behavior During Training

When a shark was shocked as it entered the end zone displaying the negative target, its body twitched noticeably. Usually it would dash away from the end compartment (escape response). Often, however, depending on the particular shark and its experience at being shocked, it would continue into the end zone despite the shock, and would turn either at the end or at some intermediate point.

During training, most sharks first developed an end association, i.e., after one or more shocks during a training period, they learned which end produced punishment and either avoided that end for the remainder of the period or, before penetrating it, displayed signs such as head-shaking which showed the end = punishment association. With most sharks, end association developed into target association with

TABLE 2

RESULTS OF DISCRIMINATION TESTS WITH BLACKTIP (B) AND GREY (G) SHARKS
(+ = discrimination; ? = probable discrimination; 0 = no discrimination;
* = simultaneous discrimination problems)

	SHARKS									
TARGETS (NEUTRAL VS. NEGATIVE)	B1	B2	B3	B4	B5	B6	B7	B8	G1	G2
No target vs. white triangle	+	—	—	—	—	—	—	—	—	—
White horizontal vs. white vertical rectangle	—	—	+	+*	+	+*	—	—	+	—
White square vs. white triangle	?	+	—	—	—	—	—	—	—	—
White circle vs. white triangle	—	—	—	0	?	—	—	—	+	—
Grey (N5/) square vs. purple square	—	—	—	—	0*	—	—	—	—	—
Grey (N5/) square vs. blue square	—	—	—	—	?*	—	—	?*	—	—
Grey (N5/) square vs. green square	—	—	0	—	—	—	—	?*	0	—
Grey (N5/) square vs. yellow square	—	—	—	—	—	—	—	+*	—	0*
Grey (N5/) square vs. red square	—	—	—	—	—	—	?	+*	—	?*
Grey (N5/) square vs. grey (N6/) square	—	—	0	—	—	—	—	—	—	—
Grey (N4/) square vs. grey (N8/) square	—	—	+	—	—	—	—	—	—	—
Grey (N4/) square vs. grey (N6/) square	—	—	+	—	—	—	—	—	—	—
Grey (N5/) square vs. grey (N8/) square	—	—	—	—	—	—	—	0*	—	+*

further training. This was shown by one or more kinds of overt responses, such as head-shaking, on seeing the negative target when displayed at either end. The criteria of discrimination have already been listed.

It was expected that learning of the target = punishment association would be followed, with further training, by learning to avoid the end zone in which the negative target was displayed (avoidance response). The avoidance response was learned reasonably well (with tests showing 0–10% of the total end-zone passes into the negative end) by only two sharks in apparently simple problems: B1, no target vs. target; and B3, horizontal vs. vertical rectangles. It was not learned by other sharks trained to the rectangle orientation problem, nor by those exposed to discrimination problems involving squares, circles, triangles, colors, and shades of grey.

Prolonged training in attempts to induce the avoidance response sometimes produced behavior which might be classed as negativistic or "rebellious," e.g., with B5. This blacktip had undergone extensive training to the circle vs. triangle problem with some signs of discrimination. During rest periods, it would circle quietly in the center zone. At the start of a training period, it would make an initial shallow pass into the end displaying the negative target, turn back and enter the neutral end, and then dash into the negative end with head shaking and body quivering.

Some blacktips (but not grey sharks) had initially, or developed during training, a tendency to circle between the center zone and one end zone. This was called an "L-bias" or an "R-bias," depending on which side was favored. Two sharks (B1 and B6) showed an L-bias during shape discrimination experiments; four (B3, B5, B7, and B8) developed a strong R-bias during color discrimination experiments. The end bias could not be overcome by persistent shocking nor, in the following instance, by offering food as a reward. B6 was being trained to distinguish between horizontal and vertical rectangles but showed persistent penetration of the L-end and avoidance of the R-end. At 1845 hours, during a rest period a piece of fish was put into the R-end, upstream of L, to induce the shark to enter. It approached the R-end with seeming interest but did not enter. At 2010 hours, while being consistently shocked at L as it entered against the negative target, it suddenly dashed into the R-end, took the fish, and then dashed back into the L-end to be shocked again as it entered.

Some blacktips displayed behavior which

might be termed "nervousness," particularly in problems involving grey vs. colored targets and, to a lesser extent, in problems involving squares, circles, and triangles. This was manifested by a hypersensitivity to incidental noises which normally did not seem to affect the sharks but which, with prolonged training, caused them to make sudden dashes and quick turns. Other signs of nervous activity were: (1) apparent agitation and rapid circling, (2) prolonged figure-8 oscillations against the wall of the tank, or (3) rapid dashes from one end of the tank to the other during which the shark would turn on its back and rub the floor. This last behavior may have been related to irritation from the tag or from copepod parasites on the back which was further aggravated by body-twitching induced by shocking. A similar behavior was occasionally seen in sharks which were not being conditioned.

In most discrimination problems, the blacktips circled with increased frequency in the safe center zone as training proceeded, thus avoiding shock at either end. This circling tendency slowed the training process and in a few cases caused us to abandon training temporarily or permanently. It did not occur with the grey sharks.

There was no noticeable difference in response between sharks subject to successive and simultaneous training techniques. Each method was used in about half of the total number of test situations (Table 2).

Despite the behavioral problems discussed above, some sharks did learn to discriminate between targets. The results are presented in the sections which follow.

No Target versus Target

The one shark (B1) presented with this problem learned to associate the target (white triangle) with shock after 36 reinforcements

TABLE 3

TIME (IN MINUTES) OF TRAINING AND NUMBER OF TRAINING SESSIONS (IN PARENTHESES), FOR BLACKTIP (B) AND GREY (G) SHARKS

	SHARKS									
TARGETS (NEUTRAL VS. NEGATIVE)	B1	B2	B3	B4	B5	B6	B7	B8	G1	G2
No target vs. white triangle	36 (2)	—	—	—	—	—	—	—	—	—
White horizontal vs. white rectangle	—	—	72 (4)	158 (11)	122 (10)	72 (4)	—	—	54 (3)	—
White square vs. white triangle	360 (19)	320 (19)	—	—	—	—	—	—	—	—
White circle vs. white triangle	—	—	—	78 (5)	486 (27)	—	—	—	180 (10)	—
Grey (N5/) square vs. purple square	—	—	—	—	180 (10)	—	—	—	—	—
Grey (N5/) square vs. blue square	—	—	—	—	108 (6)	—	—	144 (9)	—	—
Grey (N5/) square vs. green square	—	—	204 (15)	—	—	—	—	255 (18)	198 (11)	—
Grey (N5/) square vs. yellow square	—	—	—	—	—	—	—	18 (1)	—	198 (11)
Grey (N5/) square vs. red square	—	—	—	—	—	—	360 (20)	89 (5)	—	210 (12)
Grey (N5/) square vs. grey (N6/) square	—	—	108 (6)	—	—	—	—	—	—	—
Grey (N4/) square vs. grey (N8/) square	—	—	108 (6)	—	—	—	—	—	—	—
Grey (N5/) square vs. grey (N8/) square	—	—	—	—	—	—	—	96 (9)	—	216 (12)

in two training sessions. Training was continued for three more days (24 sessions, 438 min) during which time B1 consistently demonstrated that it had learned the association. In addition, it also learned to avoid the negative area with almost perfect performance.

Orientation and Form Discrimination

WHITE HORIZONTAL VS. VERTICAL RECTANGLE: Discrimination of orientation of rectangles was demonstrated by all sharks, four blacktips and one grey, presented with this problem. In training sessions extending over 1–3 days, clear signs of discrimination were shown after the following number of reinforcements: B3–127; B4–365; B5–609; B6–138; G1–120. In all cases, continued training and tests provided consistent evidence that the sharks could discriminate.

Among the blacktips, B3 and B6 with the faster rates of learning were fresh sharks which had not been trained previously, whereas B4 and B5 with the slower rates had been trained unsuccessfully to the apparently difficult circle-triangle problem (see below). The grey shark, with the fastest rate of learning, had previously been trained successfully to the circle-triangle problem.

Only B3 learned to avoid the negative end. It retained the discrimination for at least 18 days without reinforcement. A gradual extinction of the association of the negative target with shock was apparent in tests conducted after 7, 12, and 18 days without reinforcement.

WHITE SQUARE VS. TRIANGLE: Two blacktips were exposed to this problem with uncertain success in one (B1) and certain success in the other (B2). Neither shark had prior training experience.

B1 showed occasional signs of discrimination after 362 reinforcements (8 sessions in 3 days), but its behavior was too erratic to afford a firm conclusion, even after an additional 11 training sessions and a total of 629 reinforcements.

An initial attempt at training B2, involving 375 reinforcements (14 sessions in 3 days), was unsuccessful. When training was resumed after 4 days of rest, a sudden and obvious development of the associatoin was apparent after 68 reinforcements (5 sessions). Continued training confirmed the positive conclusion. Tests of retention after 5 days without reinforcement were inconclusive.

WHITE CIRCLE VS. TRIANGLE: Of three sharks presented with this problem, one (B4) failed to discriminate, another (B5) showed inconsistent signs of discrimination, and the third (G1) made the discrimination.

After 103 reinforcements in 5 sessions, B4 started to swim continuously in the center zone. Training was terminated because of the persistence of this behavior.

After 727 reinforcements (17 sessions in 3 days), B5 showed some signs of discrimination. However, an additional 305 reinforcements (10 sessions in 2 days) failed to provide further evidence.

The grey shark (G1) was trained successfully to discriminate between the circle and triangle after 476 reinforcements (10 sessions in 2 days), but it did not learn the avoidance response, even after an additional 12 sessions (216 min, 380 reinforcements in 2 days).

Color Discrimination

The training of blacktips to discriminate between grey and colored squares of the same subjective brightness (to the human eye) seemed to produce more hypersensitive and erratic behavior than was displayed in other discrimination problems. It was clear that some of the subjects discriminated between the targets, but no adequate attempt was made (by substituting different shades of grey) to determine if the discrimination was based on differential brightness or hue per se.

GREY VS. PURPLE: One shark (B5) presented with this problem failed to show any sign of discrimination after 611 reinforcements during 10 sessions in 2 days.

GREY VS. BLUE: Both of two blacktips presented with this problem showed infrequent signs of discrimination, but in neither case was it possible to reach a firm conclusion.

B5 had apparently not made the discrimination after 358 reinforcements (6 sessions in 1 day). However, two tests conducted after a period of rest provided some evidence that it could distinguish between the targets.

B8 was subjected to 2 days of training during which time it received 282 reinforcements in 9 sessions. Although it showed many signs of discrimination during training periods, tests failed to verify the positive conclusion.

GREY VS. GREEN: One blacktip (B3) and a grey shark (G1) failed to discriminate this combination, but a second blacktip (B8) showed some indications of discrimination.

B3 received 299 reinforcements (15 sessions in 2 days), while G1 received 424 (11 sessions in 2 days).

B8 showed several signs of discrimination during training (18 sessions in 3 days, with 417 reinforcements). However, tests failed to confirm a positive conclusion.

GREY VS. YELLOW: A grey shark (G2) presented with this problem failed to discriminate whereas a blacktip (B8) showed clear signs of discrimination.

G2 underwent 11 training sessions in 2 days, receiving 483 reinforcements without showing any signs of learning.

B8 showed that it could discriminate from the first of 6 training sessions (total of 155 reinforcements, 99 min) conducted in 1 day, and in a test conducted the following day. The rapid rate of learning suggests that stimulus generalization had occurred. B8 had been trained to the grey-green combination prior to training against yellow.

GREY VS. RED: Of three sharks presented with this problem, a grey (G2) and a blacktip (B7) showed only inconsistent signs of discrimination, but a second blacktip (B8) definitely made the discrimination.

G2 underwent 12 training sessions in 2 days, receiving 434 reinforcements. Occasional signs of discrimination were shown during training and concluding tests, but no decision was possible because of inconsistent behavior.

After an initial 2 days of training (13 sessions, 362 reinforcements) B7 showed some signs of discrimination. However, tests failed to confirm the conclusion. An additional day of training with 166 reinforcements in 7 sessions failed to produce more definite signs of discrimination.

In contrast, B8 showed definitely that it could discriminate after 86 reinforcements in 5 sessions. An additional 6 sessions (108 min, 189 reinforcements) and concluding tests left no doubt of discrimination.

Brightness Discrimination

Experiments on differential brightness were conducted with two blacktips (B3 and B8) and one grey shark (G2). One blacktip (B3) demonstrated the ability to distinguish between shades of grey differing by 2 Munsell units, and the grey shark discriminated a difference of 3 Munsell units.

When trained to distinguish between N5/ and N6/, B3 showed no signs of discrimination after 6 sessions over 2 days (117 reinforcements). In 6 sessions of the following day (171 reinforcements) it was then successfully trained to distinguish between N4/ and N8/. A test confirmed the positive conclusion. Another test, conducted after an additional 4 training sessions (42 reinforcements) left no doubt of discrimination. When N6/ was substituted for N8/ following the last test, it was found that stimulus generalization had occurred, and B3 reacted to N6/. However, it did not respond similarly to N5/ which was also substituted for N8/, giving a difference of only 1 Munsell unit.

B8 showed no signs of discrimination between N5/ and N8/ after 9 sessions (2 days) and 196 reinforcements.

G2 showed inconsistent signs of discrimination between N5/ and N8/ during 12 training sessions in 2 days, involving 473 reinforcements. Tests confirmed that it could discriminate. Substitution of N6/ for N8/ produced some signs of discrimination, but no firm conclusion was possible.

DISCUSSION

Training Technique and Learning

The principal aim of our training technique was to induce sharks to avoid the shocking area when they had learned to discriminate the negative target, thus producing a quantitative measure of response based on the number of passes into the neutral and negative zones. In preliminary experiments conducted in 1959, some of which involved training tanks and techniques of different design, blacktips were readily trained to avoid the negative end, especially with "easy" problems, e.g., no target vs. target, and small vs. large white targets. In the results reported here, only two sharks learned the avoidance response, and only in the apparently simple problems of no target vs. target and rectangle orientation.

Difficulty in inducing avoidance may have been due partly to the lack of obvious visual cues marking the entrance to the punishment area, such as would be provided by a partition with an opening or by a barrier in a "shuttle box" such as that used by Wodinsky et al. (1962). Another factor may have been our technique of exhibiting the negative target for prolonged periods rather than single displays. Preliminary experiments indicated that the former method, although it complicated the learning process by first developing an association with the negative *end* of the tank rather than with the target itself, still resulted in faster learning of the required associations than the latter method.

Another factor of considerable importance is the use of electric shock as an aversive stimulus. Church (1963) reporting upon the varied effects of punishment on behavior, points out that electric shock may elicit a variety of responses, including avoidance and aggression. Since some subjects learned to avoid the shock in addition to discriminating the targets in simple problems, it seems likely that their failure in other problems may have been due to the fact that the problems were bordering on the threshold of the shark's visual capabilities. This may also account for the heightened activity and hypersensitivity which resulted after continued training to "difficult" problems. Such behavior occurred frequently, making it difficult to assess visual capabilities and often forcing postponement or termination of training.

There was also a suggestion that the sharks' performance may have been influenced by prior training experience. After blacktips had been trained unsuccessfully with difficult or impossible problems, they showed a relatively slow rate of learning when later presented with easier problems, e.g., orientation of rectangles.

With continued training in attempts to develop the avoidance response, some blacktips exhibited an apparent attraction for the shock. Their behavior indicated that the punishment was anticipated, and, once shocked, they often persisted in the negative zone despite repeated shocks. Best (1963) notes a somewhat similar behavior exhibited by planaria subjected to instrumental conditioning. After having demonstrated that they could make the required choice, their performance deteriorated as they chose the unrewarded alternative and became lethargic. He notes that higher animals, particularly cats, frequently exhibit such behavior, even choosing to lie on an electric grid and receive the shock rather than attempt to avoid it. He also states that "most workers agree that it may be due to overpunishment and . . . some kind of emotional response toward the entire test situation." The behavior of blacktips, and, to a lesser extent, of grey sharks, can probably be attributed to an emotional response caused by extensive punishment in training them to difficult or perhaps impossible discrimination problems.

Visual Capabilities

It has generally been assumed that the shark eye is adapted for high sensitivity rather than acuity because of its rod-rich retina, high ratio of rods to ganglion cells, and the presence of a reflecting tapetum (Gilbert, 1963). Absence of cones in vertebrate eyes is usually correlated with poor retinal resolution and colorless vision, although Walls (1942) points out the possibility that cones may not be the sole mediators of color vision. Cones have been reported to be absent in most shark retinas examined (Walls, 1942). Recently, however, Gruber et al. (1963) found for the first time some cones in a carcharhinid shark, *Negaprion brevirostris,* and in two species of *Carcharhinus* as well. In a histological study of blacktip retinas, Kato (1962) found only a single type of visual cell, presumably the rod, despite an intensive search for a second type. He also found a high ratio of visual cells to ganglion cells. A few grey shark retinas examined were similar (unpublished). Both retinas, then, are adapted for sensitivity rather than acuity. The behavior of captive sharks indicated that they could perceive small targets from a distance of at least 5 ft and sometimes at about 10 ft, supporting the histological conclusion of high sensitivity.

Regarding form discrimination, Sutherland (1962) reports that no particular difficulties in discrimination between squares, circles, and triangles have been encountered in most animals that have been tested, including octopuses, minnows, sticklebacks, pike, and a variety of higher animals. However, he points out that the angle of rotation of the figure was frequently important; for example, he found that with octopuses, a normal square (with horizontal base as in our tests) and an equilateral triangle were easier to discriminate than a diamond (square rotated through 45°) and an equilateral triangle.

Clark (1959) successfully trained two large lemon sharks (*Negraprion brevirostris*) to associate a 16 inch square white target with food. Three nurse sharks (*Ginglymostoma cirratum*), however, failed to make a strong association. Clark (1961, 1963) also trained lemon sharks to distinguish between a square and a diamond, and between a plain white square and one with vertical stripes, but was unable to train them to discriminate a square from a circle even with the large targets used.

Our blacktips and greys readily discriminated between rectangles oriented at 90° to each other. However, in other test situations involving circle vs. triangle and square vs. triangle, only two of five sharks provided positive results. The shark's difficulty in form discrimination may be attributed to poor retinal resolution, or possibly to differential ability in learning, which, in turn, may be related to our methods. Hobson (1963) suggests that form discrimination may not be utilized by grey sharks in their natural environment. In feeding tests, he found no significant discrimination between whole baitfish (suitably slit to provide good olfactory stimulation) and decharacterized baitfish (heads and fins removed).

Clark (1961, 1963) trained lemon sharks to distinguish between a white and a red circle, and a white and a red square. As in our experiments, the luminosity factor was not eliminated.

In our tests with blacktip and grey sharks, some subjects were able to distinguish, but with apparent difficulty, red and yellow, and possibly green and blue also, from grey targets. As indicated above, it still remains a question as to whether the sharks were responding to differences in brightness or to hue. The colors were chosen for maximum chroma and, to the human eye, presented a vivid contrast with grey when viewed through water. Although the illumination was somewhat low, measuring 28 ft-c at the surface and 11 ft-c at the level of the targets, there was enough light to allow color vision, at least for animals with cone-rich retinas that have demonstrated the ability to distinguish hues. For humans, 0.01 ft-c is sufficient for photopic vision (Moon, 1961). Walls (1942) reports several workers' findings that the minnow *Phoxinus laevis* matches human ability in regard to the illumination level at which they can perceive hues. John (1964), utilizing schooling responses of *Astyanax mexicanus,* found a cone threshold in the order of 0.001 ft-c.

Eyes of blacktips and greys kept in the shark house were nearly in a completely light-adapted state: the pupils were almost slits, and the tapeta were nearly completely occluded by dark pigment. It is possible that a small increase in illumination might have raised the sharks' visual ability, as it would certainly have done for animals with duplex retinas. However, optimum light conditions for blacktip and grey sharks, with all-rod retinas, may not necessarily be the same as those of animals with cone-rich retinas.

There was no noticeable difference in learning rates or ability between the simultaneous and successive techniques employed. It has been shown (Sutherland, 1962) that the former method is more advantageous if very small differences, such as neighboring shades of grey, are to be discriminated. Using the simultaneous technique, shades of grey differing by 3 Munsell units were distinguished by a grey shark but not by a blacktip. Using the successive technique, shades of grey differing by 2 Munsell units were distinguished by a second blacktip.

Difference Between Species

No consistent differences were found in the visual capabilities of blacktip and grey sharks.

However, there was a difference in their response to punishment. While undergoing training, blacktips frequently displayed hypersensitive and erratic behavior, while grey sharks did not deviate much from their normal swimming pattern. This may reflect a real difference in normal behavior. Hobson (1963) found that blacktips were much more wary than grey sharks in their natural environment.

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REFERENCES

BEST, J. B. 1963. Protopsychology. Scientific American 208 (2):54–62.

CHURCH, R. M. 1963. The varied effects of punishment on behavior. Psychol. Rev. 70 (5):369–402.

CLARK, E. 1959. Instrumental conditioning of lemon sharks. Science 130 (3369):217–218.

——— 1961. Visual discrimination in lemon sharks, pp. 175–176. In: Abstracts of Symposium Papers. Tenth Pacific Science Congress, Honolulu, Hawaii.

——— 1963. The maintenance of sharks in captivity. Part II. Experimental work on shark behavior. Ier Congrès International d'Aquariologie, Monaco, 1960. Vol. D, pp. 1–10.

DAVIES, D. H., J. P. A. LOCHNER, and E. D. SMITH. 1963. Preliminary investigations on the hearing of sharks. South African Association for Marine Biological Research, Oceanographic Research Institute, Investigational Rept. No. 7, 10 pp.

DIJKGRAAF, S., and A. J. KALMIJN. 1963. Untersuchungen über die Funktion der Lorenzinischen Ampullen an Haifischen. Zeit. für vergl. Physiol. 47:438–456.

FRANZ, V. 1913. Sehorgan. In: Albert Oppel, ed., Lehrbuch der vergleichenden mikroskopischen Anatomie der Wirbeltiere, Teil 7. Gustav Fischer, Jena.

——— 1931. Die Akkomodation des Selachierauges und seine Abblendungsapparate nebst Befunden an der Retina. Zool. Jahrb., Abt. Allgem. Zool., Physiol. Tiere 49:323–462.

GILBERT, P. W. 1963. The visual apparatus of sharks. In: Gilbert, P. W., ed., Sharks and Survival. D. C. Heath and Co., Boston. Pp. 283–326.

GRUBER, S. H., D. H. HAMASAKI, and C. D. B. BRIDGES. 1963. Cones in the retina of the lemon shark (*Negraprion brevirostris*). Vision Res. 3:397–399.

HOBSON, E. S. 1963. Feeding behavior in three species of sharks. Pacific Sci. 17(2):171–194.

JOHN, K. R. 1964. Illumination, vision, and schooling of *Astyanax mexicanus* (Fillipi). J. Fish. Res. Bd. Canada 21(6):1453–1473.

KATO, S. 1962. Histology of the retinas of the Pacific sharks *Carcharhinus melanopterus* and *Triaenodon obesus*. M.S. thesis, University of Hawaii, Honolulu, Hawaii.

KRITZLER, H., and L. WOOD. 1961. Provisional audiogram for the shark *Carcharhinus leucas*. Science 133 (3463):1480–1482.

MOON, P. 1961. The Scientific Basis of Illuminating Engineering. Dover Publication, Inc., New York.

OLLA, B. 1962. The perception of sound in small hammerhead sharks, *Sphyrna lewini*. M.S. thesis, University of Hawaii, Honolulu, Hawaii.

SCHULTZ, L. P., E. S. HERALD, E. A. LACHNER, A. D. WELANDER, and L. P. WOODS. 1953. Fishes of the Marshall and Marianas Islands. Vol. 1. U. S. Natl. Mus. Bull. 202, 685 pp.

SUTHERLAND, N. S. 1962. Shape Discrimination by Animals. Experimental Psychology Society Monograph No. 1. W. Heffer & Sons Ltd., Cambridge.

TEICHMANN, H., and R. TEICHMANN. 1959. Untersuchungen über den Geruchssinn der Haifische. Pubbl. Staz. Napoli 31(1):78–81.

TESTER, A. L. 1963. The role of olfaction in shark predation. Pacific Sci. 17(2):145–170.

VERRIER, M. 1929. Sur la structure des yeux et la physiologie de la vision chez les selachiens. C. r. Acad. Sci. 188:1695. Paris.

VILSTRUP, T. 1951. Structure and Function of the Membranous Sacs of the Labyrinth in *Acanthias vulgaris*. E. Munksgaard, Copenhagen.

WALLS, G. L. 1942. The Vertebrate Eye and its Adaptive Radiation. Cranbrook Institute of Science, Bloomfield Hills, Mich.

WISBY, W. S., J. D. RICHARD, D. R. NELSON, and S. H. GRUBER. 1964. Sound perception in elasmobranchs. In: W. N. Tavolga, ed., Marine Bio-Acoustics. Pergamon Press, New York. Pp. 255–268.

WODINSKY, J., E. R. BEHREND, and M. E. BITTERMAN. 1962. Avoidance-conditioning in two species of fish. Animal Behavior 10 (1–2):76–78.